

## THE SEARCH DYNAMICS OF RECRUITED HONEY BEES, *APIS MELLIFERA LIGUSTICA* SPINOLA

LARRY JON FRIESEN

*Department of Biological Sciences, University of California at Santa Barbara,  
Santa Barbara, California 93106*

The foraging efficiency of a honey bee colony is maintained by workers experienced at collecting from various crops surrounding the hive. Because these experienced foragers associate the distinctive odors of flowers with the nectar and pollen rewards (Wenner and Johnson, 1966), they may be stimulated to leave the hive merely by perceiving these odors clinging to the bodies of other returning foragers or when artificially injected into the hive (Steinhoff, 1948; Johnson and Wenner, 1966). Using landmarks learned from previous flights (Wolf, 1926, 1927), these experienced bees can quickly return to those sites which they associate with the odor stimuli.

Yet, there are always some bees which lack sufficient experience to be recruited to the field by this method. Bees which have not previously collected food are continually added to the foraging population, a new crop may appear which is not in the experience of some of the bees, or a group of foragers may become idle with the depletion of a food source. Not being attached to a particular crop, these bees collectively form the potential recruit pool. By attending the dances of active foragers, potential recruits are thought to be stimulated to leave the hive in search of currently productive areas (von Frisch, 1946).

Dance attendants may be exposed to information about the feeding site in three modes: (1) tactile signals (including sounds) generated by the maneuvers of the dance, (2) gustatory signals from the offered food, and (3) olfactory signals from the odors clinging to the body of the dancing bee (reviewed in von Frisch, 1967a). However, which of this information recruits use in searching for the signalled feeding site is presently the center of controversy (von Frisch, 1967b; Wenner and Johnson, 1967; Wenner, 1971).

Von Frisch (1946) proposed that recruits rely on the quantitative information contained in the tactile signals of the figure-8 dance, while the olfactory signals merely indicate the "kind of flower frequented" by the dancer. In his summary volume (von Frisch, 1967a, page 57) he states: "When the goal is 100 m or farther from the hive the round dance is replaced by the tail-wagging dance. Like the round dance, it announces in the first place the existence of a profitable source of food, secondly the kind of flower frequented (by means of the floral odor clinging to the dancer), and thirdly the potential productivity of the food source (by means of the liveliness of the dances); and here too the scent organ is set into action on the return to the feeding place and the newcomers' locating this correctly is thereby facilitated. But beyond this the tail-wagging dance makes known the distance and compass direction to the goal, the first by the tempo of the dance, the latter through the direction of the straight segment of the run in the dance

pattern. This description of the location enables the newcomers to fly rapidly and with certainty to the indicated flowers, even when these are kilometers away—an accomplishment on the part of the bees that is without parallel elsewhere in the entire animal kingdom."

More recently Wenner has indicated that the original experiments of von Frisch lacked necessary controls. He and co-workers have proposed that, although the dance and food may be required to initiate search behavior, it is the odor associated with the dancing forager which guides successful recruits to the proper site. (See Wenner, 1971, for a discussion of this point of view.)

Conversely, other investigators have challenged Wenner and co-workers and have concluded that their data support the dance language hypothesis (Mautz, 1971; Esch and Bastian, 1970; Gould, Henery and MacLeod, 1970). But, the communication efficiencies (*i.e.*, the percentage of dance attendants successful at locating the feeding site—Mautz, 1971) obtained in these studies were only 32% (Mautz) and 13% (Gould *et al.*). Esch and Bastian reported on only those dance attendants which left the hive and found that 41% of these were successful. Additionally, for distances which should require only 30 seconds flying time, the average search times of these successful recruits were 3.2 min for 200 m (Mautz), 8.5 min for 200 m (Esch and Bastian) and approximately 13 min (but with a median value of 8 min) for 120 m (Gould *et al.*). These data indicate quite clearly that recruits did not leave the hive and fly directly to the food source. Instead, the communication efficiencies and the extended search times of recruits necessitate the accumulation of searchers in the field.

Investigators have necessarily formulated their interpretations while little was known of the flight paths or search dynamics of recruits. By assuming that recruits fly a direct path to the food source, investigators have paid little attention to the behavior of these bees. In light of the current controversy, I conducted a series of experiments between 1967 and 1970 which was designed to contrast and test the predictions of the two major hypotheses (dance language and odor dependence) while providing information on the search dynamics of recruits. More specifically, several questions were posed the answers to which would allow an approach to the primary question: What determines the flight paths and success of newly recruited honey bees?

The variables selected for testing the hypotheses were as follows: Is recruit success dependent on (1) the presence of odor in the food, (2) the number of foragers visiting the food, (3) the distance and direction to the food relative to the wind, and/or (4) the velocity of the wind within the normal flight activity ranges? If recruits can rely solely on the dance's distance and direction information between the hive and feeding site, they should be independent of the above variables; but if using only odors associated with foragers, they should be highly dependent on each of the above.

#### MATERIALS AND METHODS

This investigation of recruit search dynamics was conducted using capture techniques to sample the densities of searching bees at strategic locations. The technique used in the past has consisted of the placement of an array of dishes containing scented sucrose solution in the field while a group of foragers collected a

similar solution at a feeding station. These early experiments were designed to test the accuracy of site location by searching recruits. If, however, the searching recruits use odor as a guide, the addition of an array of odor sources would itself alter the system and dramatically influence the distribution to be measured (Wenner, 1971). Placing only a single scented station into the field after a searching population has been established should diminish this redistribution. If left for a brief period of time, a repeated use of such a monitoring station at various locations may yield a closer approximation of the distribution of searching bees. The distributions thus obtained under different experimental conditions could be compared to yield an average search pattern for a population of recruits and some of the variables which determine this pattern.

Under this assumption experiments were performed on the Lagoon Island Reserve of the University of California's Santa Barbara campus (UCSB) and at Santa Barbara Shores (SBS), 10 km west of the UCSB campus. Both sites provided large, level areas of land receiving predictable winds from the Pacific Ocean. A single hive of Italian strain honey bees (*Apis mellifera ligustica* Spinola) was used at UCSB, while the designs of experiments run at the SBS site necessitated the incorporation of a second hive containing cordovan bees (Italian strain, cordovan gene, *cd*, for body color). The cordovan bees, being of lighter color, could easily be distinguished from the darker wild type but displayed no discernible differences in behavior. In all cases two-story hives containing 50,000–60,000 bees were used.

During each experiment a single feeding station was provided for a specific number of foragers from the hive(s) involved. These foragers were trained to visit the feeding site in a manner similar to that described by Wenner (1961) and individually marked with enamel paint. All unmarked bees arriving at a feeding site were either killed by placing each in 50% ethanol with a pair of forceps or were marked as replacements of regular foragers.

Sucrose solution (1.0 or 1.5 M) was provided on vinyl-covered platforms during training and experimentation. For scented stations, an essential oil was added to the food solution. Foragers feeding on this scented solution remained lightly scented (to the human observers) even after scent was removed from the feeding station. Thus, following scented periods, unscented feeding sites remained "functionally scented" with low levels of odor provided by foragers at the station, along the flight path, and when dancing in the hive.

Glass dishes containing fresh sugar solution were placed on clean filter paper on the tabletop at regular intervals, not exceeding thirty minutes. Soiled filter paper and dishes with remaining sugar solution were doubly sealed in plastic bags and deposited in containers odor tight to humans. If an unscented period followed a scented period, the containers were removed from the area and the platforms were wiped with damp sponges.

The monitoring station used to determine the density of searching recruits did not have a fixed location but sampled various sites at different times. The locations of such monitoring sites are described separately for each experiment. This station was always scented but without regular foragers, and all bees arriving at a monitoring station were killed and tallied.

Observation periods for each experiment were restricted to morning hours be-

tween 0800 and 1230 DST, and only during these times was food provided. A variety of data was collected at the experimental (feeding) site: time, temperature, wind speed and direction, number of captured recruits, number of regular foragers, number of visitations made by these foragers, and in some experiments recording the arrival and departure times of regular foragers and the capture times of recruits was necessary. Except as related to regular foragers, the same data were collected at the monitoring station.

## RESULTS AND DISCUSSION

### *The influence of foragers on recruit success*

When altering the number of foragers which visited a dish, the amount of time that dish was occupied by a given number of bees was disproportionate to the change in forager numbers (Wenner and Friesen, unpublished observations). With ten bees visiting a feeding site 210 m from the hive, the food dish was occupied by at least three bees 63% of the time; while with five bees, three or more foragers were present only 18.5% of the time. In addition, with ten bees a vacant dish was a rare event, *i.e.*, less than 1% of the time; while with only five bees the dish was unoccupied 15% of the time.

If, as Kalmus (1954) claimed, the presence of foragers at a dish makes that site more attractive to new arrivals, then the change in the numbers of foragers visiting a site should change the efficiency of searching recruits. Thus, the recruit success rate (number of recruit arrivals/forager round trip) as a measure of this efficiency should not remain constant, but should decrease in the case of a reduction in the numbers of foragers flying between the feeding station and the hive.

To test this, the number of foragers visiting a single feeding site 360 m from the hive was varied and recruit arrivals measured. Ten bees gathered scented sugar solution (0.30 ml oil of cinnamon/liter 1.5 M sucrose) on two days. Then, the number of foragers was reduced to five, and these were allowed to forage on four days. Finally, the number of foragers again was increased to ten, and recruit arrivals and forager round trips were recorded on two more days.

These data (Table I) show that halving the number of foragers does not simply halve, but diminishes to less than one quarter, the number of recruits successful at locating the feeding site. Thus, the recruit success rate, rather than remaining constant, shows a 58% decrease indicating recruit efficiency was positively correlated with, but disproportionate to, the number of foragers visiting the feeding site.

To test whether forager presence in the field (rather than dance frequency in the hive) was sufficient to account for the above correlation, another experiment was conducted using two hives at SBS. A feeding station midway between the cordovan and Italian strain hives (Fig. 11, site III) provided 1.0 M sucrose solution scented with clove oil (0.05 ml/liter) for three hours on each day of the experiment. For three days ten bees from each hive foraged at the feeding site. Then, after a reduction to five bees from the cordovan strain hive, the station was run an additional six days. The results of this experiment are contained in Table II.

Although the number of foragers from the Italian strain hive remained constant, the recruit arrivals from that hive dropped dramatically with the reduction of



TABLE I

*The influence of the number of foragers on recruit success rates*

Date	Number of foragers	Time (hrs)	Total round trips (RT)	Recruit arrivals (r)	Recruit success rates (r/RT)
11 Aug. 68	10	2 $\frac{1}{4}$	204	41	0.19
12 Aug. 68	10	2 $\frac{1}{4}$	206	44	
20 Aug. 68	10	2 $\frac{1}{4}$	204	45	
21 Aug. 68	10	2 $\frac{1}{4}$	199	25	
14 Aug. 68	5	2	105	3	0.08
15 Aug. 68	5	2	96	9	
16 Aug. 68	5	2	125	13	
17 Aug. 68	5	2	129	10	

foragers from the other hive. With twenty bees providing feeding activity at the dish, the recruit arrival rate for the Italian strain hive was 0.46; whereas after the reduction to fifteen foragers this rate fell to 0.29. (Using the Mann-Whitney U test on the original data, these values were found to differ significantly with  $P = 0.048$ .) In addition, search times of recruits with twenty foragers were less than with fifteen. With twenty foragers the average arrival time of the fifteenth recruit from the Italian strain hive was 55 min and from the cordovan strain hive, 63 min. However, with only fifteen foragers these averages increased to 77 min for the Italian strain hive and 82 min for the cordovan bees. Again, the data suggest that the disproportionate recruit success with different numbers of foragers visiting a feeding site may be attributed to the density of these foragers in the field.

*The influence of odor on recruit success*

The magnitude of the odor dependence of searching bees was first suggested in a preliminary experiment testing the effect of odor withdrawal from two feeding sites each visited by ten regular foragers. With the stations scented, large numbers of recruits arrived; and when this scent was removed on subsequent days recruit

TABLE II

*The influence of the number of foragers from one hive on the recruit success rates of bees from a second hive. The lack of a change in the recruit success rate for the cordovan strain bees may be explained by the downwind position of their hive (see text)*

Number of days	Number of foragers	Recruit arrivals/day (r)	Forager round trips/day (RT)	Recruit success rates (r/RT)
Upwind hive (Italian)				
3	10	189.7	408.7	0.46
6	10	118.3	406.8	0.29
Downwind hive (Cordovan)				
3	10	438.7	329.0	1.33
6	5	150.7	116.3	1.30

arrivals diminished, but not to zero. By reducing the number of foragers to five at each station and maintaining the unscented condition, the recruit success rate fell to less than half (from 0.89 with ten to 0.35 with five foragers) as could be expected from the above experiments. More interesting, with fewer foragers visiting the stations, searching bees began diligently investigating the data pads and other paper near the stations! Only when foragers were at or near the dishes did these searchers approach the stations. These successful recruits paid little attention to the food on arrival, but investigated the paper towelling upon which the food dishes sat!

The paper towelling apparently had a distinctive odor to bees; and this odor, previously unnoticed by the observers at the stations, seemed to be a common factor to several types of paper. This unexpected observation emphasized the importance of location odor and resulted in later experiments being run with HCl-processed filter paper which had no demonstrable odor to bees.

Better techniques for controlling odor were initiated after the experiences of this early experiment, and the resulting data are worthy of mention. A feeding site ( $E_1$ , Fig. 2) located 360 m from a hive provided scented food (0.15 ml oil of cinnamon/liter 1.5 M sucrose) to ten foragers for two hours. The two-hour scented period was followed by two and one-quarter hours during which only unscented food was provided.

Figure 1 demonstrates the recruits' dependence on odor. With scent removal recruit arrivals virtually ceased. The occasional recruits arriving after the two-hour scented period can be explained by the low level of honey bee and location odors occurring at any site visited by bees. As evidenced by the slight decline in the forager visitation rate, regular foragers orienting to the experimental site

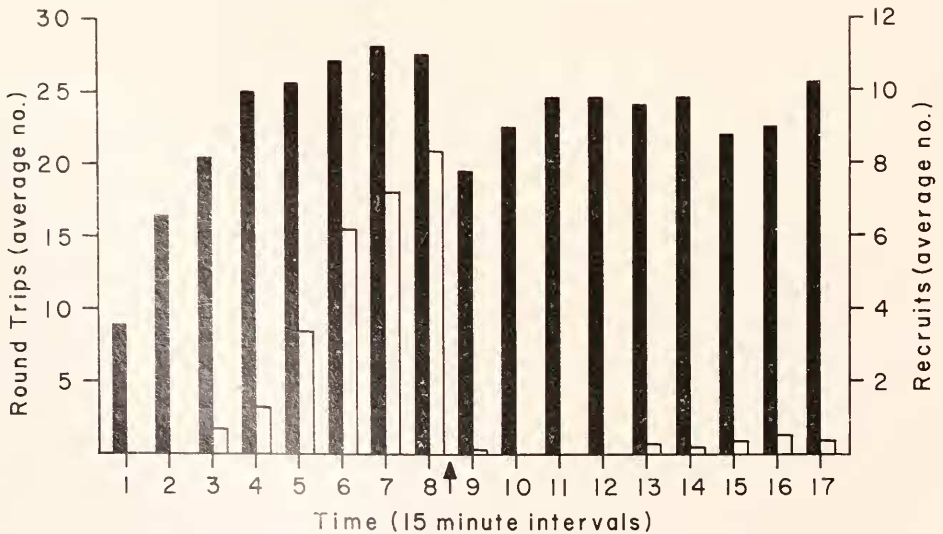


FIGURE 1. The influence of scent removal (arrow) on recruit arrivals (white bars) at a feeding site ( $E_1$ , Fig. 2) to which ten foragers were making round trips (black bars).

primarily by landmarks were influenced by odor differences as well (see also Ribbands, 1955).

Wenner, Wells, and Johnson (1969, page 84) later obtained data consistent with this result while working with unscented food in a low scent area. They reported: "That bees locate a food source by olfaction is especially possible in view of the extremely low recruitment rate of regular foragers collecting unscented sucrose at an unscented site. On 25 July 1968, for instance, in the absence of a major nectar source for the colony, we received only five recruits from a hive of approximately 60,000 bees after ten bees had foraged at each of four stations for a total of 1374 round trips during a three-hour period." (*Recruitment rate* referred to in the above is equivalent to *recruit success rate* as used in this paper.)

Since foragers dance more frequently for an unscented site (Wells and Wenner, 1971) and presumably recruit more bees to the field, the reduction in recruit arrivals after scent removal appears to be a powerful indicator of the dependence of recruits on odor for success. The recruit success rates cannot be correlated with dance frequency but support the concept of a recruit search behavior based on the odor characteristics of the feeding site. The further dependence on the number of foragers visiting a site may simply be an expression of this odor dependence in terms of bee and bee-carried odors at the feeding site and distributed by these foragers between that site and the hive.

#### *The spatial and temporal distributions of searching bees*

The spatial and temporal distributions of searching recruits were determined with Italian strain honey bees searching for one of two potential feeding sites ( $E_1$  or  $E_2$ ) at a distance of 360 m from their hive (see Fig. 2). During the course of experimentation, the wind velocity was less than 5 m/sec. The flight line flown by ten regular foragers to  $E_1$  was crossed by a southwest wind, while in a later experiment a western wind was nearly parallel to the flight line between the hive and  $E_2$ .

As mentioned earlier the addition of a single scented station within the system of searching bees should attract nearby recruits, giving a density value for that particular location. If left for a short period of time or if the earliest intervals of the monitoring periods are examined, a close approximation of the distribution of searching bees may be formed on the basis of the data obtained from several such monitoring locations.

Eleven sites separated by angles of  $22.5^\circ$  surrounded the hive at a distance of 150 m and were used to determine the radial distribution of recruits. For the determination of the longitudinal and temporal distributions of searching bees, eleven monitoring sites at thirty meter intervals directly beneath the flight path were observed (Fig. 3).

The experimental periods lasted four and one-quarter hours—a two-hour build-up period followed by two one-hour monitoring periods separated by a fifteen minute interval. During the first two hours, the system of searching bees was allowed to build up with the use of scented sugar solution (0.15 ml oil of cinnamon/liter 1.5 M sucrose) at the feeding site. Unscented sugar solution was provided at that station during the last two and one-quarter hours, while a scented

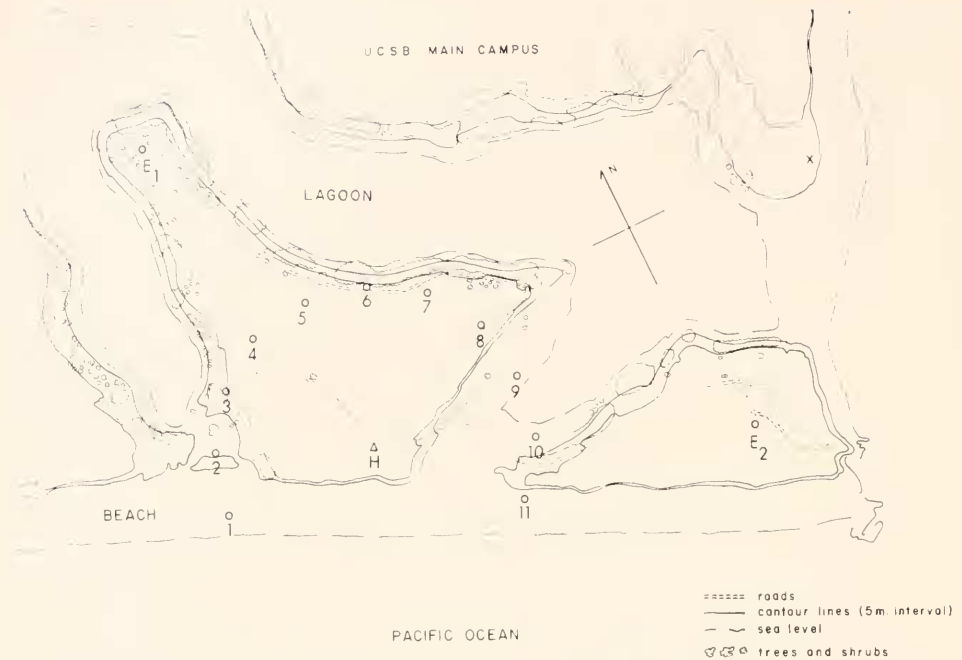


FIGURE 2. Map of the UCSB Lagoon Reserve indicating the locations of the eleven radial distribution monitoring sites (1-11), the feeding sites ( $E_1$  and  $E_2$ ), and the hive (H). The distance from the hive to the monitoring stations was 150 m and to the feeding sites 360 m.

monitoring station sampled the density of searching bees at point sources in the field. The monitoring station, located at one of the eleven selected sites during the first hour of the experimental period, was moved to a second location during the fifteen minute interval and run for a second hour. The sequence of locations thus run was determined by lot. All bees captured at the monitoring sites were killed and tallied.

As a control against the possibility that bees captured at the monitoring sites had found the unscented feeding station but were returning to the hive because of a lack of odor, the first radial distribution experiment was performed a second time with an odor plate at  $E_1$ . The odor plate consisted of a dish (like the feeding dish but screened to prevent forager contact) containing a filter paper disk kept moist with the same scented sugar solution used during the previous scented period. This dish was placed at the feeding site with the unscented dish and provided odor for the searching recruits. The conformity of the data run with and without the odor plate (see Fig. 4) allowed this control to be eliminated from other experiments.

The radial distributions obtained when using  $E_1$  and  $E_2$  as feeding sites both contained peaks lying on the flight path of regular foragers (Figs. 4 and 5). With the wind nearly parallel to the flight line between the hive and  $E_2$ , few recruits were captured at areas other than near this path (Fig. 5). However, when using  $E_1$  as the feeding site the wind was approximately perpendicular to the



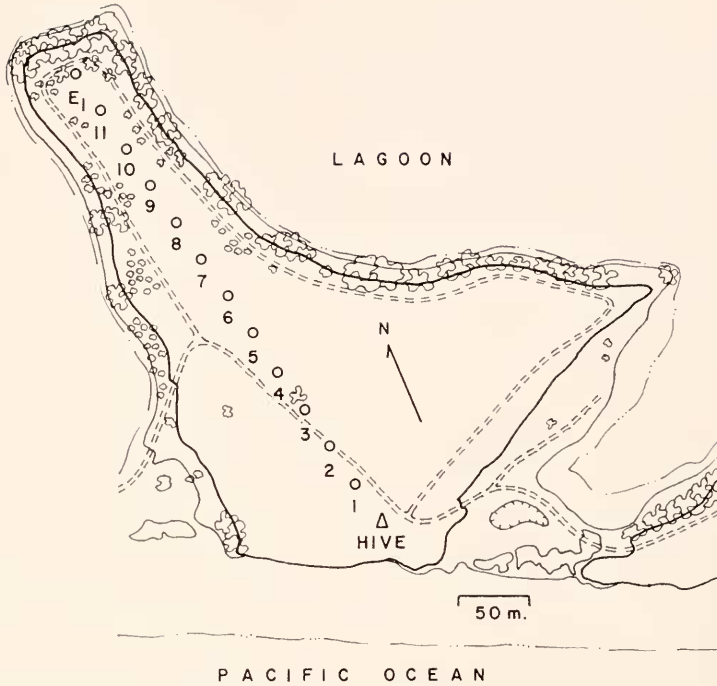


FIGURE 3. Map of the UCSB Lagoon Reserve indicating the locations of the eleven longitudinal distribution monitoring sites (1-11) and the feeding site (E<sub>1</sub>).

flight path of regular foragers, and significant numbers of bees were captured at monitoring sites upwind and downwind of this line (Fig. 4).

Apparently, searching recruits were distributed along the flight paths of regular

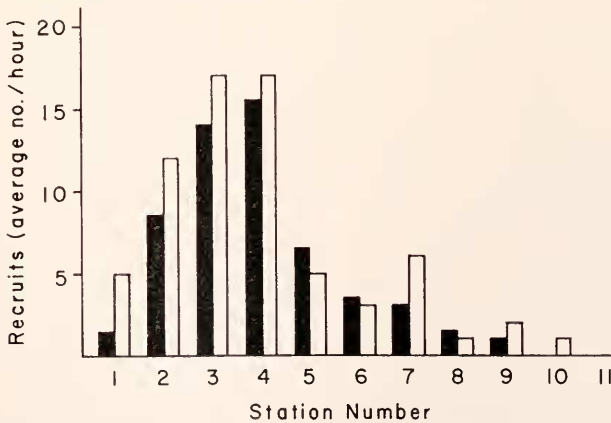


FIGURE 4. Recruit arrivals at eleven scented monitoring sites (see Fig. 2) with a forager flight path crosswind to a scented (black bars) and an unscented (white bars) feeding site (E<sub>1</sub>).

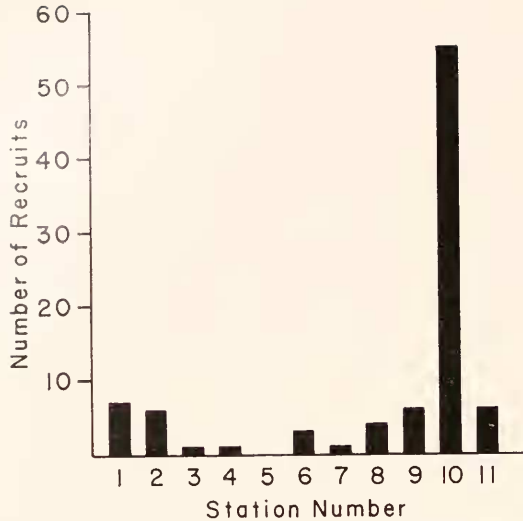


FIGURE 5. Recruit arrivals at eleven scented monitoring sites (see Fig. 2) with a wind parallel to the forager flight path between the hive and a scented feeding station ( $E_2$ ).

foragers and responded positively by flying upwind (positive anemotaxis) to the odors which they associated with these regular foragers. This behavior has been described for several insects which rely on air transmission of odor signals for site location (for a discussion of olfactory guidance, see Butler, 1967). Bossert and Wilson (1963) calculated that such behavior was necessary for efficient odor following because the extremely small concentration gradient at the downwind limit of threshold response could not be used for orientation.

Recruits arrived at upwind stations in numbers proportional to each station's distance from the flight line. Apparently, the odors from the upwind monitoring sites were windborne to the flight path and attracted recruits to these sites. Thus, the data from the experiment using  $E_1$  as the feeding site (Fig. 4) may be interpreted as an indication of the relative attractiveness of an odor source at various upwind distances (stations 1-4). When using  $E_2$ , only sites 1 and 2 were upwind of the flight path, and the number of recruit arrivals at these stations reflects their distance upwind (Fig. 5).

Of greater interest were the recruits which arrived at stations downwind of the flight line (Fig. 4). Recruits could not have been attracted from the flight line to downwind sites by odor. However, the arrival of recruits at these downwind sites may be explained if, while searching along the flight line, these bees periodically lost the odor to which they were orienting and flew downwind (negative anemotaxis) where that odor might more easily be contacted.

That this interpretation is valid may be supported by observations of recruits rapidly flying downwind after they had lost the odor of a station by drifting too far laterally or as a consequence of having flown beyond the source of odor. After such downwind flights, recruits normally reapproached from downwind on a decreasing zigzag path, presumably with the odors from the station and other bees as

cues (see also von Frisch, 1967a). This behavior occurred at the feeding site and at all scented monitoring sites in the field which received recruits. Thus, the recruit arrivals at stations 5-8 (Fig. 4) may represent the frequency distribution of distances downwind through which searchers dropped before capturing the lost odor.

These factors influencing the radial distribution of recruits are graphed in Figure 6. The distributions of points upwind and downwind of the flight line show different relationships, as might be expected from data resulting from different behavior patterns (positive and negative anemotaxis).

If odors were the foundation of recruit search behavior, the concentration of recruits along the flight line with a parallel wind should not imply communication efficiency but should merely reflect the wind direction and the resulting distribution of odors. The apparent accuracy seen in the direction of search by recruits to E<sub>2</sub> (Fig. 5) would predict a high success rate on the basis of the dance language hypothesis; yet, the downwind position of this feeding station would predict a low success rate according to the odor dependence hypothesis, since the wind would have carried the odor from this site away from the hive and the population of searching bees. In fact, far fewer recruits arrived at E<sub>2</sub> than at E<sub>1</sub>, even though the data from the latter displayed a more diffuse distribution of recruits. These data for the two-hour scented periods at the two feeding sites are graphed in Figure 7.

The eleven sites used to determine the distribution of recruits between the hive

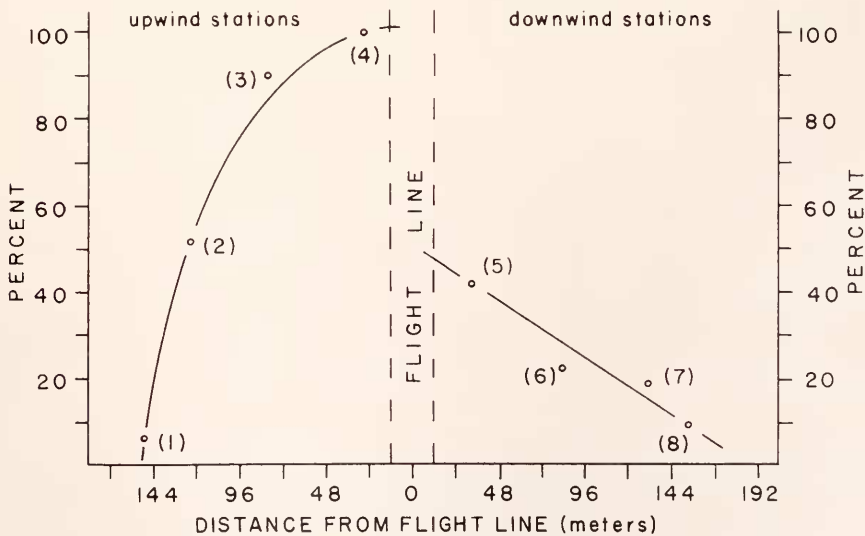


FIGURE 6. Recruit arrivals at scented monitoring stations various distances upwind and downwind of the forager flight line provided information about the influence of odor and distance on upwind flights (positive anemotaxis) and the distances downwind flown by recruits (negative anemotaxis). Each value was plotted as a per cent of the number of recruits arriving at the upwind station nearest the flight line (4). Wind velocity was always less than 5 m/sec.

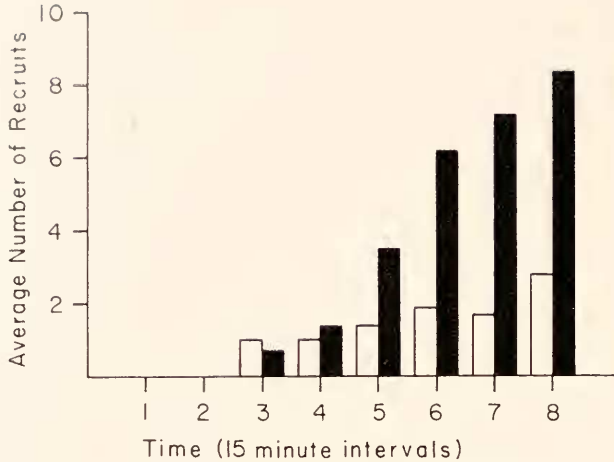


FIGURE 7. Recruit arrivals (average no./15 min) at crosswind ( $E_1$ , black bars) and downwind ( $E_2$ , white bars) scented feeding sites (see Fig. 2) without scented monitoring stations in the field.

and  $E_1$  were monitored as two groups—the even and later the odd-numbered sites (see Fig. 3). Again, a two-hour build-up period with the feeding site scented preceded the monitoring periods with the feeding site unscented. In addition to the experimental days, the feeding site was periodically monitored while remaining scented and without other stations in the field.

Because the total data for the second hour of the two-hour monitoring period conformed to that of the first for the even-numbered sites, the odd-numbered sites were run only once—either during the first or second monitoring period. This loss of data for the first hour for some of the odd-numbered monitoring sites was unfortunate, since a later analysis revealed that the data obtained during the first half hour of the monitoring period was perhaps the more important for the determination of the distribution of searching recruits.

The data of the first hour, when partitioned into half hour intervals, show an initial distribution (Fig. 8A and C) quite different from that obtained during the second half hour (Fig. 8B and D). Apparently, the data from this first half hour more closely approximated the established distribution of searching recruits, while the second half hour reflects the build-up of recruits with the change to unscented sucrose at  $E_1$ .

In the second half hour, all sites beyond 5 received nearly equal numbers of recruits when these searchers were not drawn from this area to the scented feeding station. The area of the peak in the first half hour received substantial numbers of recruits immediately, while all other stations did not attract recruits until after 10 min. Newly accumulated searchers in the area of this peak appear to have been beyond the influence of the feeding site. That this high density was formed by searchers accumulating in the field is suggested by the decreased recruit arrival rates in this area during the second half hour (Fig. 8, sites 6 and 7), even though under normal conditions recruitment increases with time (see Fig. 1).



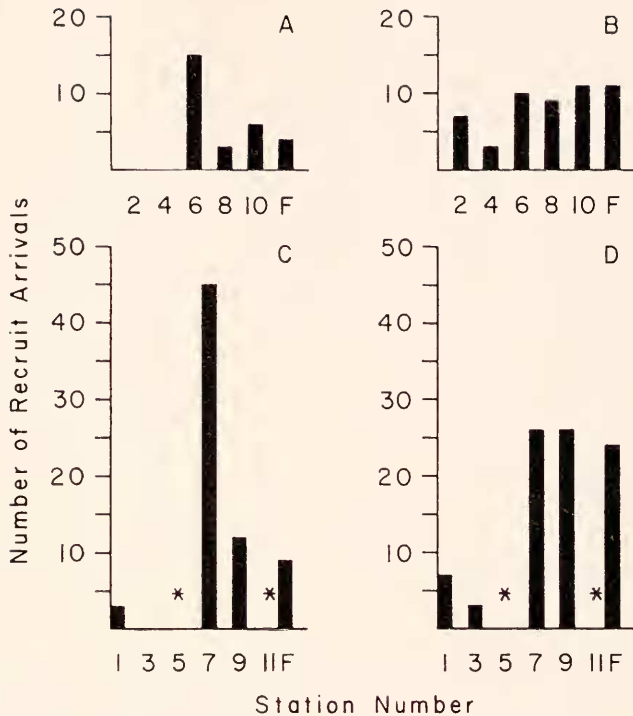


FIGURE 8. Recruit arrivals at singly-run, scented monitoring stations (see Fig. 3) compared to the feeding site (F) during the initial half hour (A and C) and the second half hour (B and D) following a two-hour build-up period. Asterisk indicates no data taken.

The distribution of the first half hour may be explained by considering that a population of searching recruits existed between site 6 and the feeding station. The removal of these bees from the more distant areas of the searching population left the highest density of searchers at sites 6 and 7. Thus, the stations, when monitored immediately after this distribution had been established, reflected the feeding station's influence. When unscented sugar solution replaced the scented solution, the feeding site no longer removed bees from the searching population and the continued presence of the monitoring station through the second half hour demonstrated the equality of attraction of new searchers to the various sites (Fig. 8B and D).

Of course under natural conditions, recruits would not be killed at the feeding place; and the searcher density would increase exponentially as these recruits recruited still others to the field. This would result in a positive feedback system with increased density leading to increased recruit success.

Even without allowing recruits to return to the hive to recruit other bees, the recruit arrival rate increases at a feeding site visited by a constant number of foragers (see Fig. 1). Wenner, Wells, and Johnson (1969) suggested that this increase, occurring at times when an increase in dancing was not exhibited in the hive, could be caused by an odor accumulation in the hive. An alternative now

would be that the increasing recruit arrival rate may be due to an increasing number of recruits accumulating along the flight line. The extended search times of unsuccessful, as well as successful, recruits (Esch and Bastian, 1970) and the data from stations 6 and 7 substantiate this field accumulation of searching bees.

With the same arrangement of monitoring sites used in the last experiment (see Fig. 3), arrival times of the first recruits were recorded at sites 3, 6, 9, and the feeding site ( $E_1$ ). Unlike the last experiment one of the intermediate stations was opened with the feeding station, both were scented, and both remained open from 0800 until fifteen recruits were captured at each site. All recruits captured were killed and their arrival times recorded. Ten bees collected scented sugar solution (0.13 ml oil of cinnamon/liter 1.0 M sucrose) at  $E_1$ ; the same solution was offered at the monitoring station.  $E_1$  was run alone one day as a standard.

Because the scented feeding and monitoring stations were placed in the field together, recruit arrivals do not reflect the distributions of established populations, but reflect the alterations of such distributions as they grew about the two odor foci. The delays of recruitment at  $E_1$  and the times of recruit arrivals at the various sites may be compared with each other and the more natural distribution seen in Figure 8. The recruit arrival times for each of the monitoring stations and the feeding site when run alone are displayed in Figure 9. The recruit arrival times for the feeding site when run alone and with each monitoring site are compared in Figure 10.

Most interesting are the large time differences for the arrivals of the first recruits at the various stations (Fig. 9). Using the feeding site when run alone as a standard, station 6 received its fifteenth recruit at about the same time as  $E_1$ ;

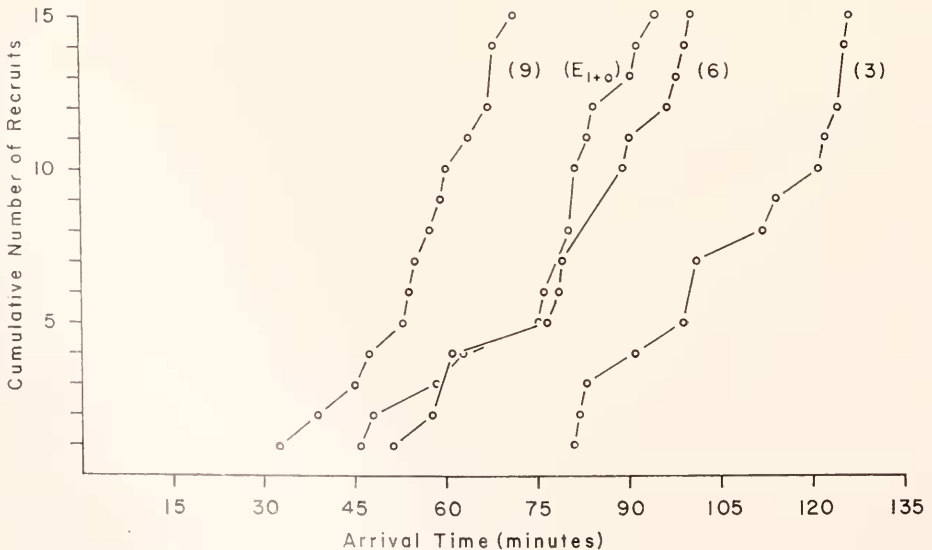


FIGURE 9. Temporal distributions of the first fifteen recruit arrivals at three monitoring sites (3, 6, and 9) compared with that at the feeding site ( $E_1 + 0$ ) when run alone (see Fig. 3).

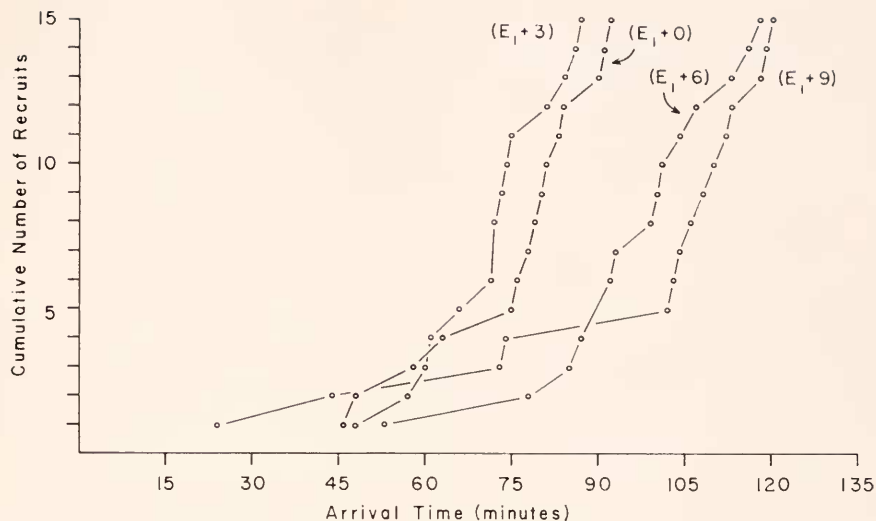


FIGURE 10. Temporal distributions of the first fifteen recruit arrivals at the feeding site ( $E_1$ , Fig. 3) when run alone ( $E_1+0$ ) or with one of the monitoring sites ( $E_1+3$ ,  $+6$ , or  $+9$ ).

while station 9 received fifteen recruits approximately 20 minutes before  $E_1$  and station 3 over 30 minutes after. Because of these extremely long intervals between the onset of recruitment at areas only a short distance apart along the flight path, one cannot assume that recruits were distracted from a direct flight to the goal. The feeding site run without intermediate "distractions" received recruits 20 minutes later than 9 and was only 90 m farther along the forager flight path. In addition, station 6, 90 m nearer the hive than 9, received recruits 20 minutes later also.

The later onset of recruitment at  $E_1$  with the accumulation of bees from the searching population at sites 6 and 9 (Fig. 10) and the long intervals between the onset of recruit arrivals along the flight path may well support the concepts of the bee density dependence of recruit arrivals and the growth and expansion of the searching population of recruits. Earlier experiments demonstrated that recruit success was dependent on the field density of foragers (Table I), even though these bees may have been from different hives (Table II). These data and the earlier arrival of recruits at sites of high bee density suggest that searchers in the field are reinforced in their efforts by the presence of other bees.

An hypothesis consistent with the data from the previous experiments suggests that a population of searching bees accumulates within an area under the influence of bee and bee-carried odors. A monitoring station placed in this population of searching bees will receive recruits in numbers and times dependent on the odor of the station and the density of bees searching in that area for the same odor. For example, station 9 placed in the center of such a distribution received the first recruits; while the feeding site and station 6 at the extremes of the distribution and at equal distances from its center received recruits later and with approxi-

mately the same delay. Station 3, outside the early distribution received recruits nearly one hour later than station 9.

Although the data suggest that it is not the dance information which guides recruits to the proper distance, the data do not suggest why recruits reject the stations closer to the hive. Perhaps a study of the scenting behavior of foragers as they approach a feeding site or of the search behavior of new recruits as they leave the hive will provide an answer.

#### *Recruit success as a function of wind*

The effects of wind were minimized in the foregoing experiments by considering data from only those days which received wind from a relatively constant direction and with a speed of less than 5 m/sec. Certainly, wind speed and direction are factors which must be considered when dealing with flying insects, especially if windborne odors may be contributing to the dynamics of their search behavior. By assuming that recruits possess preflight directions, investigators have considered wind as a complicating factor and have used "adverse wind conditions" as an explanation of data anomalous to the dance language hypothesis (*e.g.*, von Frisch, 1967a). However, if the success of searching bees is mediated by odors, then wind should not be studied as a complicating factor but as a necessary condition for recruit success. For this reason the following experiments were designed to measure the effects of wind on the success of searching bees.

Five potential feeding sites were chosen along a line between a cordovan strain hive and a hive containing the darker Italian strain bees (Fig. 11). The hives were placed so that the line of sites lay in an approximate east-west direction and, therefore, at an angle to the prevailing southeast and southwest winds. The odor from a scented (0.05 ml oil of clove/liter 1.0 M sucrose solution) station placed at one of the feeding sites and visited by a group of foragers from each hive would be carried more toward one hive than the other. In this way the two hives served as reciprocal controls.

Wind direction was determined at five-minute intervals using a wind vane; and wind force was monitored continuously with an anemometer and recorded as revolutions/min. All other data were collected as usual.

Between 18 July and 8 August 1969 the wind was consistently from the southwest, toward the cordovan strain hive. A feeding station visited by ten bees from each hive monitored the recruit arrivals at each site on four different days during two complete runs up and down the line of sites. The station was first placed at site IV and on successive days was placed at adjacent sites along the line, except at the end sites which were run two consecutive days before reversing direction. The combined data for each site are displayed separately for the two hives in Figures 12 and 13.

It is clear that wind was a limiting factor for recruit arrivals at various distances from the hives. The slight distance dependence exhibited by the cordovan strain bees from the downwind hive (Fig. 12) contrasts sharply with that of the Italian strain bees from the upwind hive (Fig. 13). Bees which searched for a feeding site upwind of the hive were more successful than those bees which searched for a site downwind of the hive. These data are consistent with those ob-



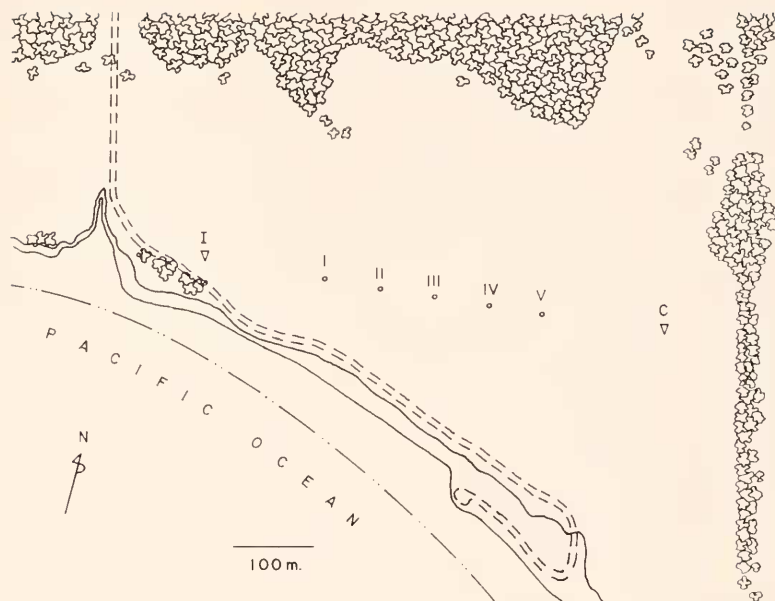


FIGURE 11. Map of the Santa Barbara Shores area indicating the locations of the five feeding sites (I-V) and the Italian (I) and cordovan (C) strain hives. The distance between feeding sites was 75 m and between hives, 600 m.

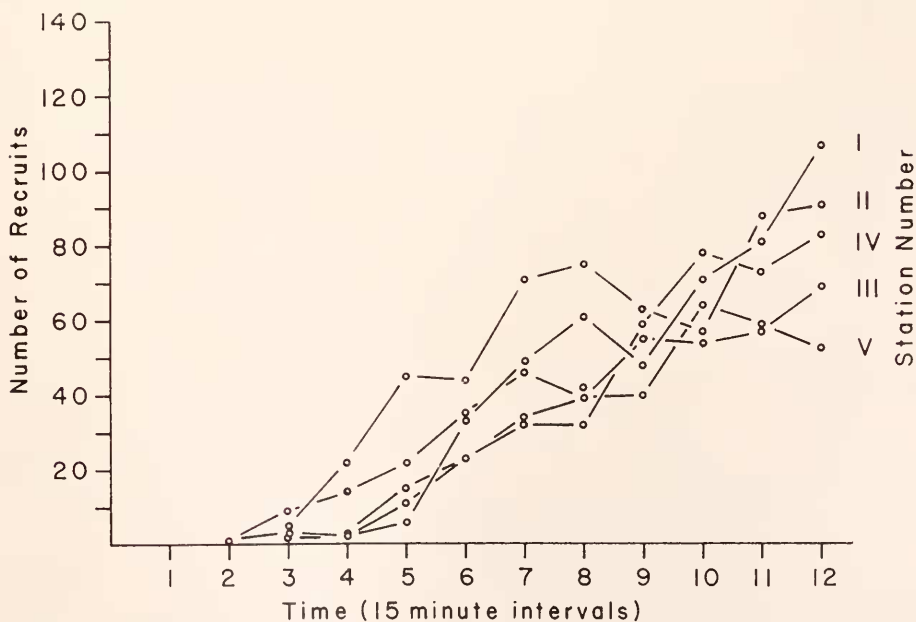


FIGURE 12. Recruit arrivals from the downwind cordovan colony at each of five feeding sites (I-V, Fig. 11) various distances from the hive.

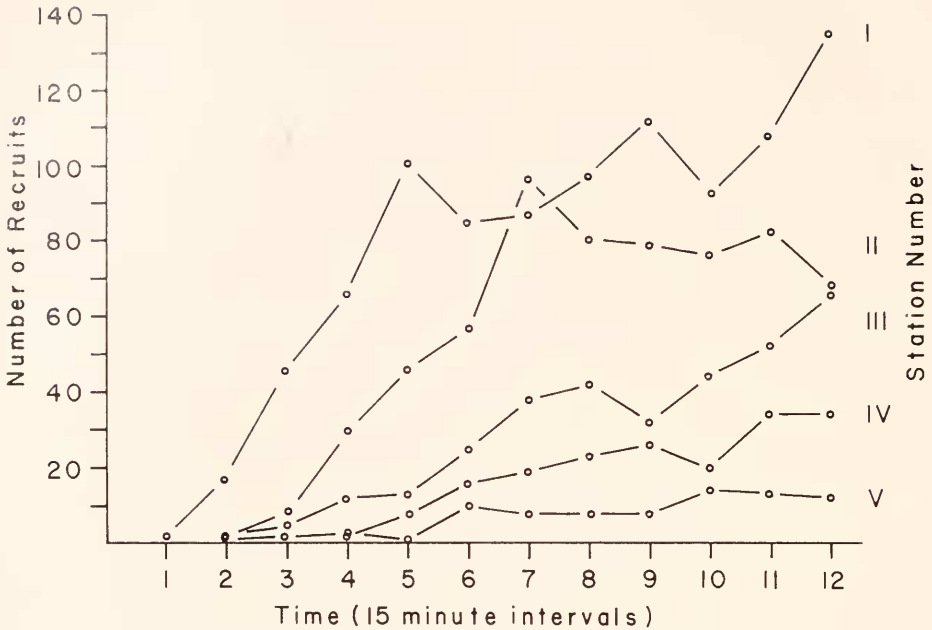


FIGURE 13. Recruit arrivals from the upwind Italian colony at each of five feeding sites (I-V, Fig. 11) various distances from the hive. Compare with the downwind hive data (Fig. 12).

tained during experiments using a crosswind and a downwind feeding station (Fig. 7) and suggest that wind direction was only indirectly important to the success of recruits, since flying against the wind aided, not hindered, their progress. Apparently, at the velocities considered wind direction was a factor only as it affected the distribution of odor and, thus, the search pattern of recruits.

The higher number of recruits which arrived at feeding sites upwind of the hive may have been a consequence of reduced search times of these successful bees. This possibility was checked indirectly by another experiment. Ten bees from each hive were allowed to forage at site III, midway between the hives, until the first recruits were captured. The temporary capture of one group of foragers then stopped the outflow of recruits from that hive; and a maximum search time for successful recruits was estimated from the arrival time of the last recruit to find the station. The later release of these same foragers allowed a minimum search time to be estimated from the subsequent arrival of the first recruit successful at locating the station. The foragers from the other hive provided feeding activity at the station and on other days served as the experimental group.

Several factors limit the reliability of these estimates. The time required to capture all foragers was as great as 3 min 30 sec; and the lack of forager flight between the hive and the feeding site after this capture created an unnatural condition for searchers remaining in the field. After the release of caged foragers, the times of the first dances were unknown. Finally, there can be no estimate of the search

times of unsuccessful recruits. (Unsuccessful recruits' flights have been given as an average of approximately 7 minutes by Mautz, 1971.)

Although the absolute value of the maximum and minimum search times may not be obtained by this method, their estimates may be compared for data collected during different wind conditions. Therefore, wind direction could be examined as a factor influencing recruit search times.

As mentioned above, feeding site III served as the experimental station at which ten bees from each hive foraged. After attaining a level of ten recruit arrivals per fifteen minute interval from the experimental hive, the regular foragers from that hive were captured and retained in a ventilated, wax-lined box. The arrival times of subsequent recruits from that hive were recorded. Following the fifteen minute interval during which no additional recruits arrived, the captured foragers were released, and the arrival times of recruits were again recorded for thirty minutes.

The data were partitioned into that group which came from a hive upwind of the feeding station and that group which came from downwind of this station. Arrivals after the capture and release of regular foragers are displayed in Figures 14 and 15, respectively. Maximum and minimum search time estimates for successful recruits are shown in Table III.

Both maximum and minimum search time estimates were shorter when the station was upwind of the experimental hive, and show a much narrower range (6:04–12:30) than did those for the station when downwind of the hive (11:20–36:10). Additionally, the arrival pattern after the release of foragers showed a more rapid acceleration in recruit arrivals to the upwind station. These data again agree with earlier observations that wind direction affects recruit success and

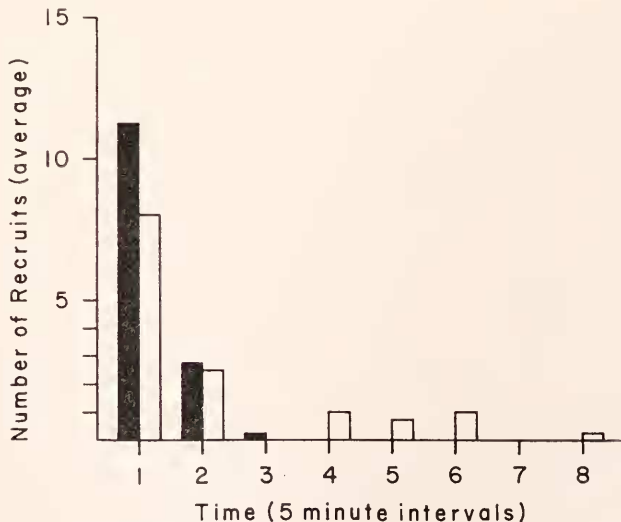


FIGURE 14. Recruit arrivals (average no./5 min) at feeding site III (Fig. 11) from the downwind hive (black bars) and the upwind hive (white bars) after the capture of their respective foragers.

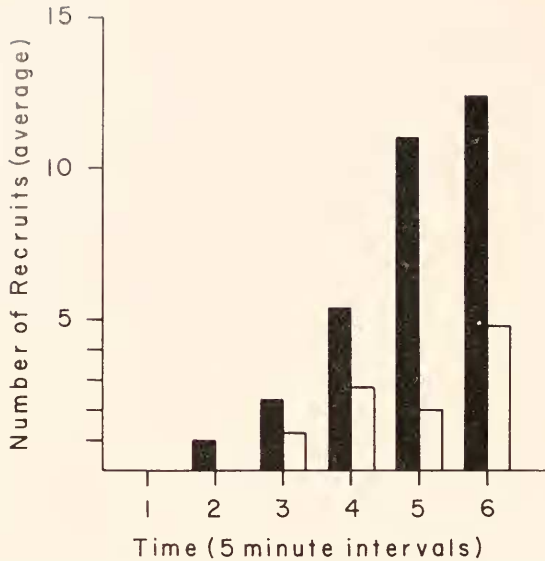


FIGURE 15. Recruits arrivals (average no./5 min) at feeding site III (Fig. 11) from a downwind hive (black bars) and an upwind hive (white bars) after the release of their respective foragers.

provides that, at least in part, this influence was due to the rapidity with which a recruit was able to locate the scented feeding site at its direction from the hive relative to the wind.

TABLE III

*Arrival times of the last recruit after forager capture and the first recruit after forager release at site III (Fig. 11) partitioned into those groups arriving from the downwind and upwind hives*

Date	Last recruit captured	First recruit captured
Downwind hive		
12 Aug. 69	6 min 4 sec	10 min 45 sec
12 Aug. 69	8 min 10 sec	6 min 45 sec
19 Aug. 69	9 min 40 sec	10 min 10 sec
21 Aug. 69	11 min 20 sec	12 min 30 sec
	Average 8.8 min	Average 10 min
Upwind hive		
14 Aug. 69	26 min 30 sec	11 min 20 sec
15 Aug. 69	36 min 10 sec	17 min 30 sec
16 Aug. 69	5 min 30 sec	12 min 10 sec
20 Aug. 69	29 min 00 sec	13 min 00 sec
	Average 24.3 min	Average 13.5 min



After observing that recruit success was dependent on the directional component of wind, the other vectorial component, wind speed, was examined as a possible factor influencing recruit success. Often during the course of experimentation, recruits appeared to arrive in clusters at times of increased wind speed. This subjective observation led to tests conducted at SBS between 23 August and 6 September 1969.

Again, site III located midway between the hives was used (Fig. 11). Ten bees from the Italian strain hive were allowed to forage at the station. During the days of the first half of this experiment, ten bees from the cordovan strain hive also foraged at this station; yet, during the last half of the experiment, only five cordovan bees were allowed to forage with the ten Italian strain bees as part of a concurrent experiment (see Table II). No other manipulation of bees except the usual killing of recruits and replacement of foragers was performed.

The data collected over a three-hour period were partitioned as a one-hour build-up period followed by a two-hour experimental period. The numbers of recruits arriving during the first and second hours of this two-hour experimental period were compared to changes in wind speed during those times. As stated, wind speed was continuously monitored using a wind speed anemometer and was recorded as revolutions per minute. The wind was always from the southwest. Data for the two hives appear in Table IV; and that for the upwind Italian strain hive is graphed in Figure 16.

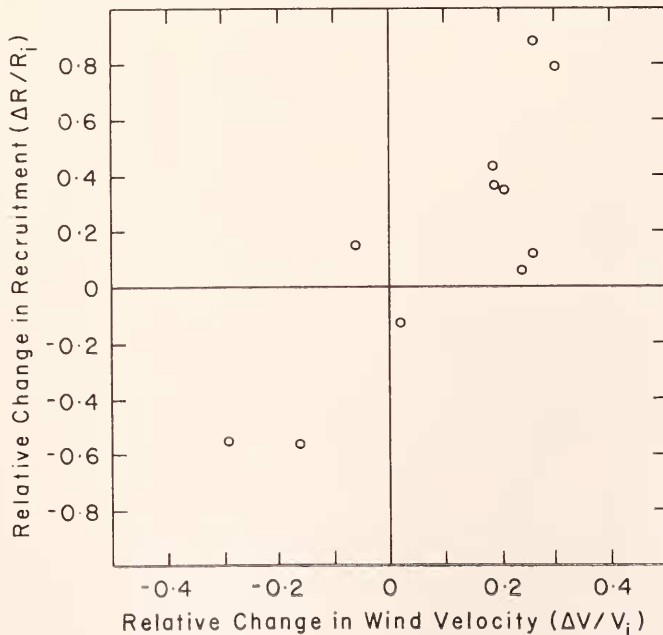


FIGURE 16. The relative change in wind velocity versus the relative change in the number of recruit arrivals to a feeding site (III, Fig. 11) from the upwind Italian strain hive (see Table IV and the text for further details).

TABLE IV

*Changes in wind velocity (V), measured as anemometer revolutions/hour, compared with changes in the levels of recruit arrivals from the downwind cordovan (C) and upwind Italian (I) strain hives at feeding site III (Fig. 11) over a two hour period*

Date	No. of recruit arrivals		No. of anemometer revolutions		R <sub>1</sub> -R <sub>2</sub> /R <sub>1</sub>		V <sub>1</sub> -V <sub>2</sub> /V <sub>1</sub>
	1st hour (R <sub>1</sub> )	2nd hour (R <sub>2</sub> )	1st hour (V <sub>1</sub> )	2nd hour (V <sub>2</sub> )	(I)	(C)	
23 Aug. 69	(I) 31 (C) 105	(I) 42 (C) 66	174.5	211.5	0.35	-0.37	0.21
24 Aug. 69	41 91	18 56	237.5	199.5	-0.56	-0.38	-0.16
25 Aug. 69	39 133	45 102	278.5	262.5	0.15	-0.23	-0.06
27 Aug. 69	87 67	39 79	282.0	203.0	-0.55	0.18	-0.28
28 Aug. 69	40 33	35 39	124.0	127.0	-0.13	0.18	0.02
31 Aug. 69	32 84	34 102	303.0	376.0	0.06	0.21	0.24
1 Sep. 69	14 32	19 61	328.0	389.0	0.36	0.91	0.19
3 Sep. 69	14 26	20 47	222.0	264.0	0.43	0.81	0.19
4 Sep. 69	28 16	50 33	188.0	245.5	0.79	1.06	0.30
5 Sep. 69	26 42	49 37	309.0	389.5	0.88	-0.14	0.26
6 Sep. 69	34 51	38 63	220.0	274.0	0.12	0.24	0.26

The cordovan strain hive data showed no obvious correlation between changes in the level of recruit arrivals and increases and decreases in wind speed. This would be expected on the basis of the upwind position of the feeding site from this hive. Since bees are able to compensate for changes in wind velocity and maintain a relatively constant ground speed (Wenner, 1963), searchers downwind of an odor source need only exhibit positive anemotaxis upon perceiving the proper combination of odors to quickly reach the goal. The successful recruits from the cordovan strain hive, having flown upwind to the odor source, display this anticipated lack of wind speed influence.

The Italian strain recruits, on the other hand, travelled downwind to the odor source and had their progress influenced by wind speed changes. These recruits were less successful than cordovan strain recruits; but within this group, bees searching during higher wind speeds were the most successful (Fig. 16). The exhibition of negative anemotaxis by searchers after odor loss offers an explanation for this wind speed dependence.

The bee and bee-carried odors from the flight path of foragers would be carried more toward the feeding site than the hive. Recruits searching downwind of the flight path would perceive the odors from foragers flying toward the feeding site as pulses of odor, since these odors would be trailed as a front at an angle to the wind's direction. On the other hand, recruits following odors from foragers flying toward the hive would be led back to the hive on a continuous trail.

Outward flights of foragers would be responsible for the recruits' progress toward the feeding site. With the perception of each odor pulse, searchers would immediately orient upwind and lose the scent. Thus, the subsequent downwind flights after each odor loss would bring these bees nearer the goal. Higher wind speeds would allow longer downwind flights, and these longer flights would be responsible for the shorter search times exhibited.

*Search dynamics: odor, dance, and the scent gland*

There is now a substantial body of evidence which demonstrates complex interrelationships among the variables of the recruitment process. Those variables seen to have the greatest importance to recruit success are the initial dance, food odor, forager density in the field, and the vectorial components of wind. Wenner and Wells (in press), working with foragers performing disoriented dances, have shown that at least the direction information of the dance is not necessary for recruit success. Odor, however, is apparently crucial to recruit success. The further dependencies of recruit success and distribution on the field density of foragers carrying this odor and the vectorial components of wind distributing this odor suggest a recruitment system based on windborne odor trails between the feeding site and the hive.

The apparent accuracy in the direction and distance of search by recruits now seems to be due, not to preflight information enabling a direct flight to the food source, but to the association of recruits with the odors from the forager flight path and the feeding site itself. The extended search times of flights repeatedly taken by unsuccessful, as well as successful, recruits demonstrates the accumulation of these bees within a searching population outside the hive. As a consequence these data have failed to support the dance language hypothesis.

Apparently positive feedback systems operating on the accumulated searching population enhance the ultimate success of recruits searching in the field. Certainly, the cumulative attractiveness of an area with increasing bee density is an example of such a system. The disproportionate increase in recruit success with increased bee density at the feeding site and the earlier arrival times of recruits at stations placed within a high searcher density suggest some communication among bees in the field as the foundation of this positive feedback system.

Because recruits frequently display Nasanov gland scenting as they approach monitoring stations and orient to the exposed Nasanov glands of both foragers and recruits near these stations and the feeding site, it may well be that the odors from this gland serve as a link among foragers and recruits in the field. Although not necessarily an attractant (Wells and Wenner, 1971), Nasanov gland scent may orient and reinforce recruits searching in the presence of odors to which they have been conditioned. Thus, the distribution of the searching population would initially be dependent on the odors from foragers and the feeding site while the growth of this population would allow later recruits to orient to these other searchers—a positive feedback system enhanced by the cumulative influence of new recruits.

Wells and Wenner (1971) have reported evidence suggesting that both forager dancing in the hive and Nasanov gland exposure in the field are dependent on the size of the potential recruit pool. Their interpretation (page 207) was: "unsuccessful recruits not only contribute to Nasanov gland exposure through their contact with oriented foragers in the field, but these unsuccessful recruits also return to the hive and contribute to an enlarged recruit pool. Presumably, contact with numerous available recruits induces successful foragers to dance, leading to the correlations we have observed." Thus, two positive feedback systems coordinating the enlargement of the searching population with increased scenting along the flight

path and near the feeding site could be controlled by and lead to the success of the searching population.

Although speculative this interpretation compares favorably with the observations of temporal distributions of recruit arrivals along the forager flight path. Conceivably, the concentrations of both forager and food scent near the feeding site accounted for the higher density and earlier arrival of recruits at areas of the outer half of the forager flight path. Apparently, the growth and expansion of the searching population with its growing influence on foragers and new recruits was responsible for the progression of recruit arrivals in both directions along the flight path from the area of earliest recruitment.

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#### SUMMARY

Some variables in the recruitment process of honey bees were studied as they affected the distribution and success of the searching population in the field. The dance language and odor dependence hypotheses were contrasted and their predictions compared with the following observations.

1. Recruits were attracted to the odors from the food which were carried by foragers and were dependent on these odors for success.

2. A monitoring of recruit densities in the field demonstrated an association of searchers with the forager flight path.

3. The degree of correspondence between the distribution of recruits and the direction of the flight path to the feeding site was correlated with wind direction, not search efficiency.

4. Feeding stations upwind of the hive provided the highest recruit success rates, shortest search times, and the least dependence on wind speed. Downwind stations provided the lowest recruit success rates, the longest search times, and the greatest dependence on wind speed.

5. A disproportionate increase in recruit success with an increase in the number of foragers visiting a feeding site was correlated with the density of the foragers in the field.

6. Increased bee densities at the feeding site, even with bees from different hives, increased recruit success and shortened search times.

7. The progression of and the extremely long intervals between the onset of recruit arrivals at areas along the forager flight path suggested communication among bees in the field and a dependence of recruit success on the density and growth of the searching population.

These observations are compatible with an odor dependent search behavior and together fail to support the predictions of the dance language hypothesis. Dance attendants appeared to have been conditioned to the odors associated with re-

turning foragers and, after leaving the hive, entered a searching population dependent on these odors for success. The dependence of recruit success on food odor at the feeding station, the density of foragers between this station and the hive, and the direction of the wind indicates that the integrity of the forager flight path was extremely important to this success. The distributions and extended search times of recruits indicated a search behavior based on positive anemotaxis during the perception of the proper combination of odors and negative anemotaxis after the loss of this stimulation.

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